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The temperature dependence of the development of the
embryo In Mesocyclops leuckarti (Claus) and
Cyclops scutifer Sars

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Diagrams XI + XII show least for time of development of eggs
at different temperatures for each species .

Introduction

This work is mainly intended as an addition to the studies of the populations dynamics of Cyclops scutifer, which is part of the "Latnajaure project" (a study of the principles involved in the ecosystem of a small -initially fish free- mountain lake, before and after the introduction of fish). It was given as a "three unit" problem in zoology, under the direction of docent (lecturer) A.Nauwerck at the Limnological Institute in Uppsala, where the laboratory work was done from the end of May till mid November. The field work consisted of sampling in lake Erken in Roslagen in June, July and September, as well as in Latnajaure in the Abisko mountains in August and September of 1965. Additional sampling was done in Latnajaure for the study of the horizontal, vertical and temporal distribution of Cyclops scutifer, as well as the in situ development of the different stages. These samples have been analysed in such a way as to fit into the frame work of future studies on the population dynamics of Cyclops scutifer. The main aim of the present investigation is the determination of the dependence upon temperature of the development of the embryo in the subarctic Cyclops scutifer as compared with the conditions found in the warm water Species Mesocyclops leuckarti.

I would like to thank Professor W.Rodhe for the great privilege to do my laboratory experiments in the constant temperature rooms of the Limnological Institute. I would also like to give my warmest thanks to docent A.Nauwerck for directing the work, and to docent B.Pejler at the Zoological Institute for interest and good advice.

Materials

Mesocyclops leuckarti was collected in lake Erken, which is situated about 50 km East of Uppsala. The area of the lake is about 2285 ha and the mean depth is about 9 m, and it could be classified as moderately eutrophic. Collections were made with a plankton net with a mesh-size of 200 μ . All net samples were taken at the deepest part of the lake(about 21 m), and each time both horizontally and vertically. I generally made a quick preliminary sorting of the material on the spot. It was then transferred to a thermos bottle and transported by car to Uppsala. Further work with the material was then, if possible, done immediately, but it was necessary under certain circumstance to postpone some of it till the following day, and the animals were then kept at 2°C overnight.

Sampling at Eken was done on 12/6, 15/6, 1/7, and 2/9 1965. On these dates the temperature varied between 15° - 17° at the surface and 10° - 12° near the bottom, except for 2/9, when the lake was nearly homothermal.

Cyclops scutifer was collected from Latnja jaure, which is situated 12.5 km in a straight line to the west of Abisko tourist station, at an elevation of 978 m. The area of, the lake is 74 ha and its mean depth is 16.5 m, and it could be described as extremely oligotrophia. Samplings were done with the same type of net and in the same way as described earlier. I. did not find it necessary to take the samples at the deepest part (43.5 m), close to a steep cliff, where avalanches and falls into the lake may occur at least in the beginning of the summer, but was satisfied with a 30 m depth. The. samples were put in ½ litre plastic

bottles with a screw lid and were immediately put into a specially built icebox refrigerator for the transport to Uppsala, where work could start on the material 2 - 3 days later.

Samplings at Latnajaure were done on 16/8 and 23/9 1965. The temperature of the water on these dates was about 4° respect. 5° and the lake was homothermal during this time.

As it was impossible to start all the experiments with Cyclops scutifer at the same time, because of difference in time of sampling and the difficulty to obtain fresh material from Latnajaure, I was forced to keep the animals in aquaria. The aquaria were illuminated and at 8°C. The animals were fed in two out of the four aquaria. The food consisted of pure cultures of Chlamydomonas.

Earlier experiments have shown that Cyclops scutifer can produce new eggs under laboratory conditions (Nauwerck, personal communication). But it was possible that the egg production in the aquaria would not proceed at the same rate as in the lake and the eggs would be too old. Material from these aquaria was therefore only used for experiments started within a few days. A difference in the egg production in the aquaria with the addition of Chlamydomonas as compared to those without could not be established with certainty.

The material from the second sampling in Latnajaure did not at all have eggbearing females, but the production of eggs could be instigated in the laboratory by the addition of different nutrients. To test the feasibility of different algae as food,

several test tubes, in addition to the aquaria, were started with membrane filtered (millipore HA 0.45 μ) Latnja jaure water, each containing about 30 animals. The animals were fed with resp. Cryptomonas, Chromulina and Chlamydomonas (cultures from the Limnological Institute). In addition tests were made with water from the waterlily pond in the Botanical Garden, which contained a rather rich natural phytoplankton, as well as membrane filtered Latnja jaure water alone.

The egg production started after about a week in most of the test tubes, but it never reached great quantities. But distinct differences were noted. The natural phytoplankton from the lily pond was apparently the best source for food, next best, for the egg production was Cryptomonas, while Chlamydomonas proved to be less suitable. In cultures with Cryptomonas the animals died off first.

The eggs from these experiments were used for all the following and complementary experiments.

Methods

For the determination of the length of time for the embryonal development in planktonic animals, two methods are available. The first one (method 1) has mainly been used by Elster (1954), Eichhorn (1957) and Eckstein (1964) for various calanoid copepods. It consists of isolating newly laid eggs or females with newly laid eggs, and keeping these under observation at constant temperature until the eggs are hatched.

The advantage of this method is that one can exactly

determine the time of development for single eggs as well as the time interval between the first and the last hatched egg in an eggsac. Further, one does not have to separate the eggs from the females but one can maintain as natural a condition as possible. The draw-back of the method lies in the many replications necessary to determine individual aberrations and to ensure against losses. One must keep a rather large number of ripe females under continual observation in order to isolate them as soon as they have laid eggs, and as it is also difficult to obtain a large quantity of eggs of exactly the same age, really young age, different experiments have to be started at different times.

The other method (method 2) was suggested by Edmondson (1965} who used it for plankton rotifera. The method assumes that a growing population contains eggs of all stages of development and new eggs are continually being produced. A great number of eggs and respective egg sacs - regardless of stage of development - are isolated from the females and kept at a constant temperature. The number of hatched eggs is determined at short intervals. In this way the rate of development of the eggs in a mixed culture (population) can be determined, regardless of the age of individual eggs. The time of development is obtained by plotting the number or percentage unhatched eggs against time and determine the median(average) line, and where this line cuts the abscissa, the last egg should have been hatched. The method

thus gives a uniform material to work from and does not demand any lengthy preparations or extensive experimental arrangements. It should in addition give good statistical means. The main draw-back of this method lies in the often very time consuming countings, especially as with cyclopids, where two eggsacs must be considered as one statistical unit. It is further easier to create an unfavourable culture condition with a very concentrated sample, and the risk of loss is here greater than in the first method.

I have mainly used the second method as it is simple to execute and can be applied directly, but I have also used the first method as control.

In general, I have for each experiment used eggs from about 80 females(equivalent to about 800 - 1400 eggs) and distributed these in two counting chambers, about half filled with membrane filtered water from the corresponding lake. The chambers consisted of glass cylinders with a diameter of 36 mm and height of 100 m² with a cover glass at the bottom end.

Glass beakers, turned upside down were used to cover the tops, as these allowed circulation of air. The division into two cylinders was a safety measure against mishaps and it also made counting easier. Counts were made with an inverted microscope (the Utermöhl microscope), where the cylinders can be placed so that the material on the cover glass bottom can be studied without disturbing the distribution. The counts were, as far as possible, made at the respective experimental temperature: the cylinders from 5° and 14° had to be counted at 8°.

Following table shows the temperature and the frequency of checking.

	25	20	14	8	5	4.5	2
ops	6x/24hr	2x/24hr	2x/24hr	2x/24hr	-	1-2x/24hr	1x/1-3 2 4h
i	-	1-5x/24hr	1x/24hr	1-2x/24hr	1x/1-2 2 4hr	-	1x/2-3 2 4hr

The frequency of checking was determined by some preliminary experiments, before the start of the main experiments. The time interval was generally shorter at the beginning and later modified according to need. The above table also covers experiments with method 1. By using the first method, the intervals can obviously be longer at the beginning but shorten as the hatchings proceed.

The number of unhatched eggs was also counted each time with the number of hatched, and a note made of the dead ones. Dead nauplii as well as empty naupliar skins were counted when they occurred.

The experimental results are presented as a quantity/time diagram where the percentage distribution of hatched, unhatched and dead eggs can be read off for each case. With the aid of these diagrams the time of development is calculated for the various temperatures. The individual times of development are then summarized in graphs, which give the relationship between temperature and time of development in the two species studied.

Before starting the criticism of the methods in general, it is of some interest to discuss further method 2. The method assumes, as pointed out earlier, that the material consists of a mixture of all developmental stages in equal proportions, from newly laid eggs to those that are ready to be hatched. Such a mixture should be found in an environment where polycyclic species occur, especially in warm biotopes while no other factors inhibit the reproduction. It is rather more doubtful if this is the case with cold biotopes, where there is a reason to assume that the

species present are mono- or oligocyclic (with one or more short periods of reproduction). My experiments have shown the former to be true for Mesocyclops leuckarti ,but the latter for Cyclops scutifer. In order to get some idea of what and how much the results obtained with method 2 can reveal, I shall discuss the method from a theoretical point of view, starting with certain assumptions (fig. 1) .

In the first case (a) we assume that we have a uniform and fresh material. In the beginning no hatching is recorded, but later when it starts all eggs are hatched within a very limited time. T corresponds to the average time of development and Δ is the statistical dispersion (scatter) for individual eggs. The slope of the curve is thus only a measure of this scatter but not one of the rate of development in relation to temperature.

In the second case (b) we assume a well mixed starting material. The hatching occurs more or less continually. If the material consists of eggsacs, the curve will most likely be stepped as eggs in an eggsac are hatched more or less at the same time. Even a material consisting of single eggs will show the points of observation to be scattered around an average line. The point where this average line intersects the abscissa again gives T , while Δ can be obtained by lines parallel with the average line and following the scattering of the points of observation around the latter. The points of intersection of these parallel lines with the abscissa give the statistical scattering of the time of

development for single eggs and egg sacs respectively. The slope of the curve (middle(average) line) is a measure of the rate of development.

In the third case (c) we assume that we have a material of the same age but older. As with the first case, we have no hatching at all in the beginning and then the whole material is hatched at about the same time. But if we do not know how old the eggs are, we cannot determine T . The statistical scatter Δ comes out right, but is hardly of interest by itself.

In the fourth case (d) we start with a mixed but older material -ere the curve will show too short a time of development ($T - X$). The slope of the curve is useless as a measure of rate of development, but can unfortunately not be distinguished from the "right" one.

In the fifth case (e) two different assumption could give the same curve. The material either originates from two different species, varieties or such, one with a shorter, the other with a longer embryonal development (for which both T s can be determined, the longer time directly (T_{A1}), the shorter after a simple correction (T_{A2}), or the material has earlier been Influenced by a higher temperature, which shows a delayed action in the first phase of the curve. In the latter example, the right time can be obtained by a parallel displacement (B.) of the faulty slope (A_1).

In the sixth case (f) we do not assume that all eggs will be hatched but take into account the mortality. The lower curve

gives the percentage of eggs which die during the experiment. Though the mortality is constant the percentage of dead eggs will increase exponentially, but one must assume that during a long time and under artificial conditions, the mortality itself will increase. The mortality curve will influence the hatching curve, especially during long experiments, so that the latter is bent upwards and finally cut off by the mortality curve. When the experimental time is not too long the intersection point T_1 can be considered as equal to T . During long experimental duration, and a strongly increasing mortality curve, one runs the risk that all eggs will be caught up by death before they finish their development. In this case the first phase of the hatching curve can perhaps still show the true slope which can be extrapolated for the determination of T .

Of the above discussed cases, which of course may occur in whatever combination in a natural material, the two first represent the ideal case for both our methods. Case a needs no further comments, it is relatively easy to realize it. On the other hand, one most likely comes frequently across combinations of cases b to f, and the question raised whether it is wise to draw conclusions from such experiments. In my experiments, secondary errors were sometimes so great as to mask phenomena according to case c to f, even though I knew that they must have occurred. The dispersion(scattering) in the results was caused not only by the developmental time of individual eggs, but also by the difficulty to assess dead eggs, counting errors, and losses due

bacterial decomposition. With due consideration for all the known errors, it was still possible to obtain the times of development in a satisfactory way.

Criticism of the methods

Although the experience with these two methods has been good, they have certain inborn weaknesses. The most important objections to them are as follows.

It is possible that differences occur in the rates of development of eggs from different (cyclopid-) generations during the course of the year. It might perhaps be possible to assume that eggs could be pre-embryonally affected through factors of the environment, for example the temperature which the female and the ovary has been exposed to. It is further not out of the question, that the general physiological condition of the female might influence the rate of development of the egg (cf. for example resting eggs in certain planktonic animals!). Elster (1954) studied the rate of the egg-development in Eudiaptomus gracilis Sars in Bodensee on material from April, August and October and November and found no significant differences between the material from the different times of the year. I have also not been able to find such differences.

It is, on the other hand, obvious that small and large eggs occur within the same brood, and that the smaller (yolk-poor) usually have a considerably longer time of development. It is possible to think that the eggs in a poorly fed population might be smaller and thus be slower in their development.

Elster (1954) and Eichhorn (1957) give at least an indication of this possibility. This objection might hold true for Mesocyclops leuckarti from the September samplings, when the eggs (and indeed also the animals) were smaller than from those in June/July, and the low number of eggs - only 4 - 5 per sac, as compared to 7 - 9 in the early summer - might indicate a lesser supply of nutrient.

It is also possible that the eggs of very old (perhaps also of very young) females might have similarly bad characteristics. The laboratory cultures of Cyclops scutifer, when the last experiments with their eggs were started, consisted solely of old females. Their eggs were also small and few in number and the high mortality one would indicate an inferior quality. Then there is the question about the importance of the quality of the water in the test tubes in having an effect upon the rate of development. Elster and Eichhorn have shown that the chemistry of the water (within the limit of fresh water) has no effect on the rate of development of several calanoid copepod eggs. This most likely holds even more so true for the cyclopids, which are well known to be more robust. But I must leave unanswered whether the high mortality of the eggs which I observed in my experiments, certainly not corresponding to that found under natural conditions, was caused only by bacterial activity, and not by chemical factors. It must in both cases be assumed that the eggs can in principle be attacked and even a mild attack might result in a slower development.

To this can be added errors in the counting itself, in counting the same twice, in omissions, in confusing dead eggs for hatched eggs and the difficulty in general in the determination of dead eggs (compare the variation in the total number of eggs in appendix 1 - 23 and the fluctuations in the the hatched and respectively dead eggs in the diagrams!). These errors can be reduced by training, but can hardly be completely eliminated.

Finally there is an obscure error, whereby, during longterm experiments, both dead eggs, empty eggshells and perhaps also dead nauplii and naupliar skins rot away and are never counted.

Results

The experimental results obtained at the different temperatures can be read from diagram I - X. By expressing the total number of eggs as 100% (disregarding possible fluctuations of this number due to errors in counting, etc.) the curves have been made comparable. The area between the upper base line (100%) and the curve for hatched eggs represents the portion of hatched eggs in the sample. The area between the lower base line (0%) and the mortality curve gives corresponding portion of dead eggs, the area between these two curves, which gradually becomes narrower, represents the unhatched, living portion of the eggs. Parallel experiments are drawn individually in the diagrams. Experiments using method 1 are also represented in the same way.

The time interval at which the egg hatching terminated was determined in relation to the shape of the curve and the condition of the experiment in general. In certain cases the time interval

was delimited to a few hours, but especially at the lower temperatures, where the curve for hatched eggs at the end of the experimental period had very much levelled off, and where a high percentage of death made very difficult the determination of the time at which hatching definitely stopped, the time interval has been made rather long so as to play it safe. Another factor affecting the length of the time interval is the frequency of checking. Experiments checked every three hours offered of course a better opportunity to delimit the length of the time interval to several hours, as opposed to those checked once in 24 hrs.

Mesocyclops leuckartix, comments on the curves

I was able to obtain fresh material for all the experiments, as Erken is not far from Uppsala, and there was no need to keep the animals in aquaria cultures. The curves also show that the material was obviously well mixed, the hatching is in all cases continuous, and the values for parallel experiments differ very little. The results can thus be considered reliable.

The temperature which showed the lowest egg mortality and highest egg hatching respectively can, with certain reservations, be considered as the optimal temperature for the species. It appears to be close to 20° for Mesocyclops leuckarti. The maximum temperature, thus the temperature at which the animals still would develop, was not determined. The rate of development was still increasing at 25° C, bad effects were not observed neither among eggs nor the hatched nauplii, and still higher temperatures (at which Mesocyclops

leuckarti may well occur under natural conditions) were not available.

The lower temperature limit, on the other hand, could be determined at between 8° and 4.5°. Experiments were done at 4.5° and 2° but at neither of these could normal hatching be found. A certain amount of hatching occurred at the beginning, but it stopped soon afterwards, which indicates that the hatching which took place was caused by previous higher temperatures. One experiment at 4.5° C was terminated after 9 days as all unhatched eggs were judged dead. The other test tube was left and checked at certain intervals. No further hatching was found during a further 9 day period and the experiment then terminated. The same results were found at 2°, thus first some hatching then stagnation and death. In order to determine if the eggs were really dead or just dormant at the low temperature, they were put back at room temperature where a few days later all eggs were found to be dead.

In the experiment at 25° (diagram 1), one test tube (A) contained as usual filtered lake water, and the other (B) tap water. Unlike the earlier cited experiments by Elster and Eichhorn, a considerable difference was found between these parallel experiments. The mortality percentage was considerably higher for both eggs and nauplii in the test tube with tap water, but the hatching was faster and the nauplii which survived exchanged their "skin" earlier. The question, whether this really was an effect of the water and if so what the underlying cause was, must here be left unanswered.

The difference between the parallel experiments at 20° (diagram II), and the sine-shaped curve, was most likely caused only by the statistical dispersion and is of no significance.

There is a good agreement between parallel experiments at 14° (diagram III) and 8° (diagram IV). The faster development observed in experiment E at 14° , was most likely caused by the mortality curve having in reality already earlier retarded the development (broken line). A more rapidly rising mortality curve is to be expected at 8° (broken line).

Of the most credible gradient is constructed for each curve, taking into account that the material in the beginning of the experiment could have been influenced by temperatures to which it had earlier been exposed and at the end of the experiment by the increasing mortality, then the intersection point of the slope with the abscissa agrees surprisingly well with the time interval during which the hatching actually terminated. The experiment at 8° is the only exception, where the slope requires a large correction on the observed final value. But this correction is plausible considering that the time of development at 4.5° is approaching infinity (If the slope for the few hatched eggs is reliable, then the time of development at 4.5° should be about 4 months, if the eggs survive till then).

Cyclops scutifer, comments on the curves

It was not possible to perform the experiments with Cyclops scutifer with fresh material only. The experiments at 8° and 20° were started with the animals from 16/8 immediately upon arrival

in Uppsala. With the experience gained of the fast development in Mesocyclops leuckarti, I deemed it necessary to check the experiments at 20° every three hours. This, in addition to checking the test tubes at 8°, made it impossible to start any further experiments at the same time.

The rest of the animals were, as mentioned earlier, kept in aquaria cultures for later experimental use. Unfortunately, it did not emerge till later, when plankton samples collected at different times were studied, that the animals were nearly synchronized in their development, as opposed to Mesocyclops leuckarti. The whole population had laid its eggs within a very short time, more or less during the second and third week in August. The eggs were thus of about the same age, which means that the slope of the hatching curve can not be used as a measure of the rate of development. The end point alone can be used to determine the developmental time, with perhaps some certain corrections regarding age and prehistory of the material.

In these experiments I had to assume that the material consisted of a large number of old and a fast decreasing number of new eggs. Theoretically, the curves should approach the final value asymptotically. But the same picture emerges also because of the influence of the mortality curve. There were most likely some fresh eggs at the beginning of the experiment, but I must assume that they were so few that their chance of survival as a group was little and none of these were for sure the last hatched egg in the sample.

It is therefore possible that the experiments at 2° and 5°, which were started 4 - 5 days later, might show a shorter time of development than ought to have been at these temperatures. In addition, the eggs did not appear to be in as good a condition as when the first experiments were started (perhaps supported by the unusually high mortality in these experiments), and I considered it unsuitable to start still later experiments with this material using the same method. The experiments at 14 were done according to method 1 and solely based upon eggs produced in the laboratory.

In accordance with the earlier way of reasoning (p.8) the optimal temperature for Cyclops scutifer must be around 8°. Here it was also not possible to determine the maximum temperature. The results from 2° and 5°, on the other hand, show clearly that the eggs of Cyclops scutifer, as opposed to those of Mesocyclops leuckarti, will develop at these low temperatures and the minimal temperature for embryonal development in Cyclops scutifer is close to 0°.

Material used for the experiments at 20° was partly "mixed" fresh material and partly eggs reared in the laboratory. The time of development was slightly longer for the laboratory material, where all eggs were newly hatched. The mortality was high, and about the same in both cases and shows that the eggs did not develop under optimal conditions. Taking into consideration the possibility of rather a too high average age of the eggs in

in experiments L and M and the sharp increase in the slope of the mortality curve, the results from experiment N must be considered as the most correct (which indicates a corrective addition of 20 - 30 hours to the results of L and M).

At 14°, where all the eggs were new, the final values can be considered reliable. The observed differences were most likely caused by the individual scattering of the rather sparse original material.

The best hatching was obtained at 8° and the final values may also be considered reliable. Considering the experience from the experiments at 20°, the results must also be corrected by the addition of 20 - 30 hours, or the upper limit for the area of terminated hatching must at least be considered as the most reliable.

In one of the parallel experiments (experiment U) at 5°, the eggs show a considerably shorter time of development and in the beginning a much steeper slope on the curve for hatched eggs (diagram IX). This was caused by a mishap with one test tube, which had to be replaced by a new one, and the eggs had at that time been at 8° for a further few days. The first phase of the curve shows the same slope as the curves at 8°. But it is possible to calculate the necessary correction (added in the final diagrams, XI - XII). The samples were kept at 3° for five and respectively ten days before the experiment started. At 8° the time of development including corrections, is about 380 hours or 16 days. This

would mean that the eggs in both experiments at 5° had gone through 1/3 and respectively 2/3 of their development before the start of the experiment. The time must therefore be increased by 50% and 200%. The most likely time of development is thus between 500 and 650 hours.

The same 50% correction should be applied to. the experiment at 2°. The time of development would thus be about 1000 hours. Because the mortality is high here (it most likely follows the broken curves) the time of development is very likely still longer. The slope of the curve intersects the base line close to 1000 hours, the addition of 50% gives 1500 hours as the final value. This value seems reasonable when compared to the values for the higher temperatures. A correction of at least double the experimental value must be allowed for. Further errors may have been added when the temperature was not kept constant because of a break down in the thermostat, which allowed the temperature to fluctuate between the extremes of 0° and 4°.

The rate of development of the first naupliar stage

As naupliar skins are easily observed in the experiments, these as well as dead nauplii were noted. The time span between the first hatched eggs and the occurrence of the first naupliar skins should give a reliable measure of the life span of the first naupliar stage at the various temperatures. The later stages become more complicated but these will not be discussed here. The number of dead nauplii in relation to hatched eggs can give a measure of the well-being of the species in general

under the prevailing experimental conditions and especially under
 (transl. ?)
 the temperature used. When the naupliar mortality is very low,
 so that, for example, in the beginning of the experiment all the
 nauplii die immediately after the hatching, then the timespan
 between the the first hatching and the occurrence of the first
 naupliar skins can of course not be used as a measure of the life
 span of the nauplii, but the time between the first definite sur-
 plus of living naupli and the occurrence of skins must be chosen.
 If the development proceeds in definite waves, then it is possible
 within the same experiment to measure the distance between several
 peaks for hatched eggs and naupliar skins.
 The following table gives the time span in hours at different
 temperatures.

	<u>Mesocyclops leuckarti</u>	<u>Cyclops scutifer</u>
25°	34 - 39	-
20°	49 - 53	(60 - 97)
14°	83 - 91	72 - 73
8°	>290	195
5°	-	?
2°	-	?

Naupliar skins of Mesocyclops leuckarti were not found at 8°
 during the experimental time, in spite of abundance of nauplii
 and a low mortality percentage. The life span of the first naupliar
 stage must therefore exceed 290 hours.

It is difficult to get a clear picture of the time involved
 at 20° for Cyclops scutifer. As the mortality amongst the nauplii
 is very high, it becomes difficult to judge to which of the newly
 hatched eggs the skins belong. The value given in the table could
 because of this be erroneous. It is possible that one has to

consider the long time as resulting from the inferior conditions of living for Cyclops scutifer at that temperature.

It is in general rather striking that the naupliial mortality is much higher for Cyclops scutifer, at an average 70% of the hatched eggs as compared to 30% for Mesocyclops leuckarti, which would indicate a rather greater sensitivity of Cyclops scutifer.

It is of interest to note that the development of the nauplii is faster for Cyclops scutifer than Mesocyclops leuckarti, especially at lower temperatures. The quotient from the time of egg development: the time of naupli development is in general lower for Mesocyclops leuckarti than for Cyclops scutifer, but as the temperature decreases this quotient increases for Mesocyclops leuckarti whereas it decreases for Cyclops scutifer.

Conclusions

The curves in diagram XI and XII combine the time of egg-development at different temperatures for both cyclopoid species and a more detailed comparison is possible.

The most striking result is the much faster embryonal development at the higher temperatures for Mesocyclops leuckarti than for Cyclops scutifer, with the development of the latter taking about three times longer, but the curves for the two species cross over at about 6°, when the eggs of Cyclops scutifer develop faster than those for Mesocyclops leuckarti. In the vicinity of 5° the curve goes asymptotically towards infinity for Mesocyclops leuckarti, the development of eggs is nearly halted, whereas this does not happen for Cyclops scutifer till below 2°.

As the curves can not be exponential functions (though their middle part appears roughly to follow such a function) but must be optimum curves, a renewed increase in the time of development could be expected close to the maximum temperature for the species. In practise, the very increased mortality at the high temperatures appears to stop development before the curve is able to change. Only for Arctodiaptomus salinus (Daday), Elster et al. (1961), has it been successfully shown that the developmental time increased at higher temperatures. It is possible that my material does show such a change in the curve for Cyclops scutifer. The most reliable developmental times at 14° and 20° are identical, which in practise should be equivalent to a relative increase in relation to the higher temperature. The suspicion that the optimum for the rate of development must be between 14° and 20° is supported by results from the nauplii.

My results thus confirm fully the opinion that Mesocyclops leuckarti is a warm water form: the eggs of the species develop well even at temperatures not encountered in our natural waters, but typical for sub-tropical and tropical waters. The optimum for the rate of development of eggs must lie above 25°, and it is possible that the maximum might even be above 30°. The species obviously lacks the ability to develop even at moderately low temperatures, a further property which forces Mesocyclops leuckarti to seek a warmer environment (in the temperate lakes it survives the cold time of the year by the diapause).

One becomes rather more sceptical about the accepted characterization of Cyclops scutifer as a typical cold water form.

The species can Indeed still develop at very low temperatures, and can thus dwell in cold water. And its developmental optimum lies definitely lower than for Mesocyclops leuckarti,.but it - does lie much higher than the average temperature, and even higher than the maximum temperature of the biotopes, among which Cyclops scutifer is usually found.

One must conclude that in warmer biotopes Cyclops scutifer is not able to compete successfully and is finally pushed out by species which are capable of faster development. The average temperature usually accompanies the nutritional standard: the warmer the water, the richer it, in general, is in nutrients, and increasing temperatures in general mean increasing availability of food. The species which can. utilize the impending offer of nutrients by quickly building up a large population at the higher temperature, have thus the best opportunity to colonise warm (and normally nutrient rich, eutrophic) biotopes and oust slower species, assuming that not other factors are limiting. Vice versa, the species is better off in cold (and normally nutrient poor, oligotrophic) waters, which is not "fooled" by short term temperature

increases, which are not accompanied by an appreciable increase in available nutrients. A species which under such conditions reacts at once by mass reproduction would soon be exposed to very Inferior conditions of living and die of starvation, caused by the competition, which it itself started. Were this to be repeated several times, then the species must disappear from the biotope, as no animals can reach maturity.

Cyclops scutifer must therefore be considered as a cold water form not because it prefers cold biotopes, but because it can not compete in a more favourable environment due to its slower development. It is exactly this slow development which becomes an asset in the cold biotopes.

Comparison with the literature and discussion

The dependence of the embryonal development upon temperature has in recent years been studied in several calanoid copepods, for example, in Eudiaptomus gracilis Sars by Sister (1954) and Eckstein (1964), Eudiaptomus graciloides(Lillj.) by Nauwerck(1963), Acanthodiaptomus denticornis Wierz. and Mixodiaptomus laciniatus Lillj. by Eichhorn (1957) as well as Arctodiaptomus salinus (Daday) by Elster et al. (1961). Studies on cyclopids are only found in some older works, namely by Walter (1922) on Megacyclops viridis (Jurine) and by Ziegelmayer (1925) on Macrocyclus fuscus (Jurine).

By first comparing my results with results of other cyclopids, the most striking difference is the short time of development at low temperatures found in the earlier studied cyclopoid species (all non-planktonic). Walker gives the most complete data and according to him the developmental time should only be 15 days for Megacyclops viridis eggs at 1°. Also Ziegelmayer's data indicate similar short periods at low temperatures. Neither of the abovementioned authors give detailed information about their methods, especially not with regards to the temperature and temperature stability (the word thermostat is not mentioned),

and as the temperatures are also reported as average temperatures, one may wonder, if this fast development was not partly due to variations in temperature during the experimental period. The development is not proportional to the various temperatures, as the curves are not exponential functions.

If the values from the older works are reliable, then they give an interesting example of the adaptability of pond species to their special environment in contrast to pelagic forms. Ponds usually have a plentiful supply of nutrients even during the cold time of the year (the more so as these pond forms often stay at the bottom) so that a fast development is always advantageous.

My material agrees better with the calanoid copepods. But the pelagic cyclopids rate of development at low temperatures than the calanoid species. All the species studied agree very closely at higher temperatures, at 20° the time is about 2 days for all except Cyclops scutifer.

Acanthodiaptomus denticornis and Mixodiaptomus laciniatus agree somewhat better with Cyclops scutifer in their demand for environment, they are monocyclic and are mainly found in oligotrophic and cold waters. Eudiaptomus gracilis and Eudiaptomus graciloides agree better with Mesocyclops leuckarti, they are polycyclic and are found in more eutrophic waters. The embryonal development in the respective species also appears to agree: it is faster at low temperatures in the cold water forms as compared to the warm water forms.

Nauwerck (1953, p. 65) considers Mesocyclops leuckarti in Erken to be a monocyclic form. Figure 34 shows at least two

distinct maxima for egg laying females. Comparing these to the actual temperature and making due allowance for the time of development of the eggs it seems very probable that the species complete more than one cycle per summer. The size difference which I observed between the females in samples from June/July and from September emphasizes that at least two generations should occur in the lake.

One further problem will be touched upon here. Lindström (1951, 1958) and Axelson (1961) proposed the theory that Cyclops scutifer occurs in two so-called "fractions", namely populations at different time of the year, which definitely differ from each other as to size and should also have different life cycles. Nauwerck (pers. comm.) thought at first that also the Latnja jaure Cyclops were divided into these fractions, but concluded after more detailed measurements that the size difference between the animals was a fleeting effect in this lake. I have treated my material as a unity and the results indicate nowhere that fundamental differences are present between the eggs.

I shall finally discuss in the light of my results the importance of Cyclops scutifer as fish food in relation to the impending introduction of fish into Latnja jaure. It is not certain whether such a small species as Cyclops scutifer is used as food by full grown fish, but at least the fish fry should be able to use it as food. I found a good sized population of Cyclops in Latnja jaure (10 - 30 individuals per litre), which might appear to be a good source of food for fish, but it is more likely not so

because of the slow development of the species. The population is most likely not renewed once a year. The lake is ice-free for two - three months and the maximum temperature in the summer of 1965 was not much above 5°. Eggs laid in the lake at about 10 - 20

of August, were thus hatched in the beginning of September, and it is very improbable that the nauplii passed beyond the copepodite stage the same year, and it is possible that the last hatched nauplii did not even make it during the following year.

Summary

1. The dependence upon temperature of the embryonal development was studied in Mesocyclops leuckarti (Claus) from lake Erken in Roslagen and in Cyclops scutifer Sars from Latn ja jaure in the Abisko mountains.
2. Two methods were used. According to method 1, newly laid eggs are checked until they hatch, according to method 2, the hatching is checked at different time intervals in a large number of eggs. Method 1 gives time of development directly, whereas method 2 gives rate of development, from which time of development can be determined. Method 1 is more reliable and more time consuming, method 2 simpler but assumes that the egg material is a homogeneous mixture of all stages of development.
3. Experiments at constant temperatures were done with Mesocyclops leuckarti at 2°, 4.5°, 8°, 14°, 20°, and 25° and entirely by method 2; with Cyclops scutifer at 2°, 5°, 8°, 14°, and 20° and by method 2, except for all experiments at 14° and part of the 20 experiments, which were done by method 1.

4. The temperature for the highest frequency of hatching (optimal temperature) was at 20° for Mesocyclops leuckarti, and at 8° for Cyclops scutifer. The minimum temperature for embryonal development lies between 8° and 4.5° for Mesocyclops leuckarti, and below 2° for Cyclops scutifer. The optimum temperature (where development proceeds the fastest) was above 25° for Mesocyclops leuckarti, and between 14° and 20° for Cyclops scutifer. The maximum temperature could not be determined for either species. About 30% of the hatched Mesocyclops leuckarti nauplii died during the experiments and about 70% of Cyclops scutifer.

5. Above 6° is the increase in the rate of development larger in Mesocyclops leuckarti, but below 6° larger in Cyclops scutifer. These results were interpreted as giving an advantage in competition for Mesocyclops leuckarti in warm and nutrient rich waters, and for Cyclops scutifer in cold and nutrient poor waters.

6. The comparison with the literature shows that the temperature dependence of the embryonal development in Mesocyclops leuckarti and Cyclops scutifer agrees better with that of the pelagic calanoid forms than with the cyclopoid pond and littoral forms.

Figure 1

→ tid : time

The ordinate shows the percentage of unhatched eggs.
The abscissa shows time.
Each ring represents one observation.

Diagram I - XII

Rör : test tube (cylinder)
tim : hours
veckor : weeks

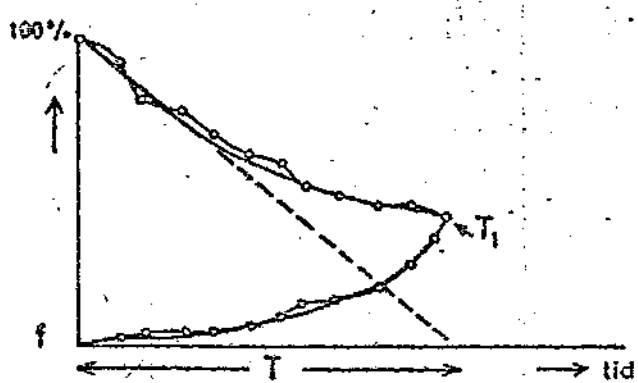
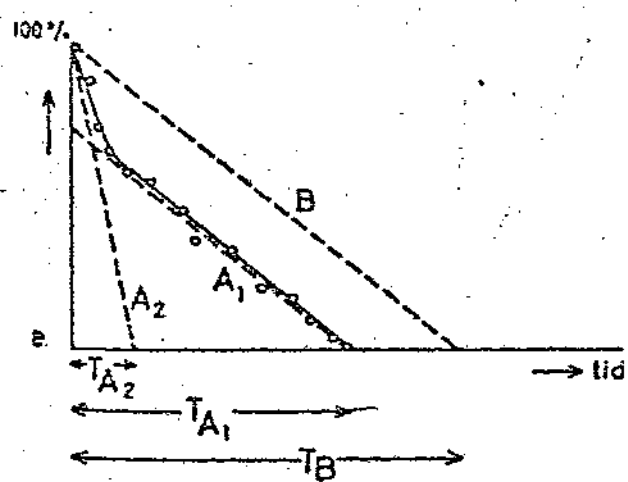
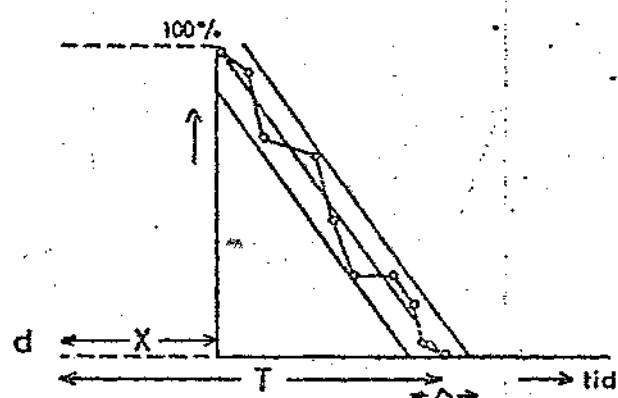
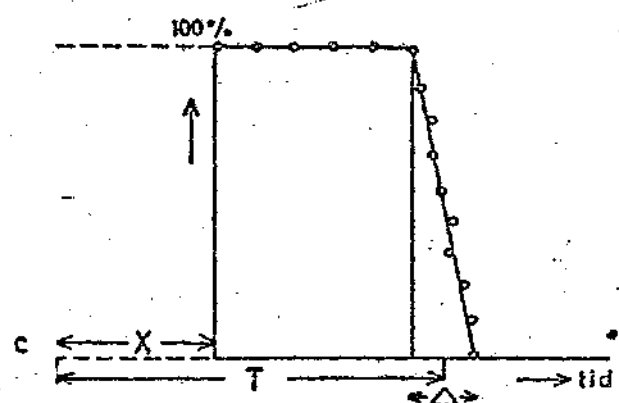
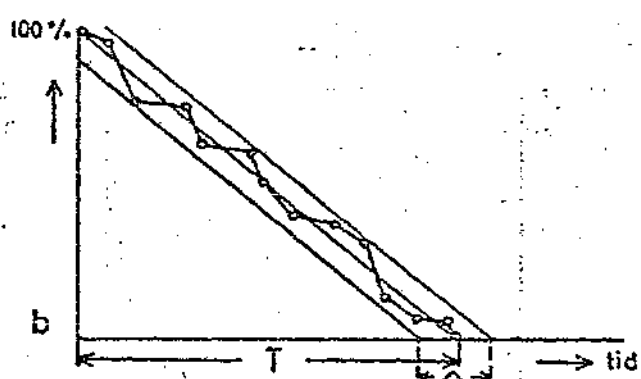
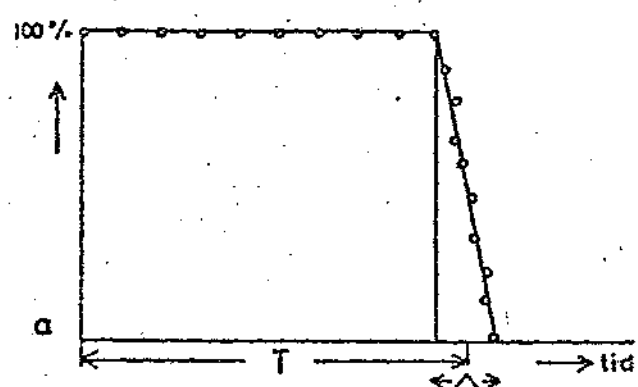
Bilaga : appendix 1 - 23
Försök : experiment
förs. start. : experiment started
dag : day
tid : hour(time of day and night)
okläckta ägg : unhatched eggs
kläckta ägg : hatched eggs
döda ägg : dead eggs
döda nauplier : dead nauplii
naupliehudar : nauplial skins
summa ägg : sum of eggs
% okläckta ägg av : % of unhatched eggs of
% kläckta ägg : % of hatched eggs of
% döda av : % dead of

Appendix 21

röret ramlat och tömts. Nytt rör satt 29/8 kl 14:30 : the test
tube broke and was emptied. A new test tube started on 29/8 at
14:30 o'clock.

Litteraturförteckning

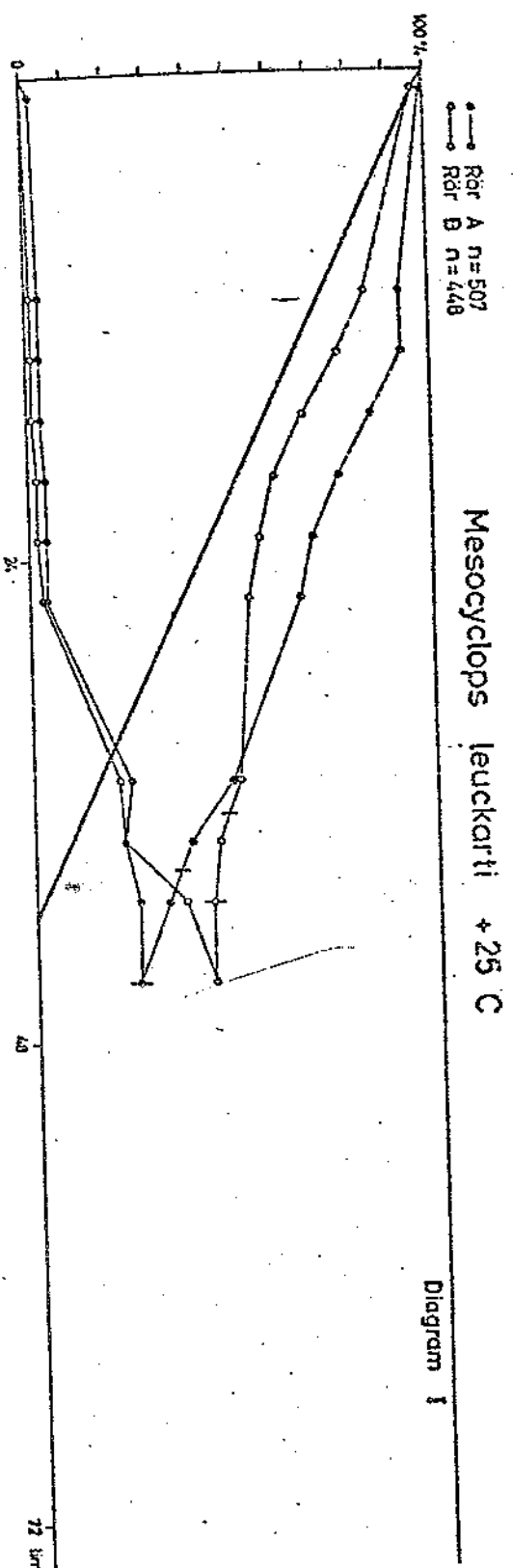
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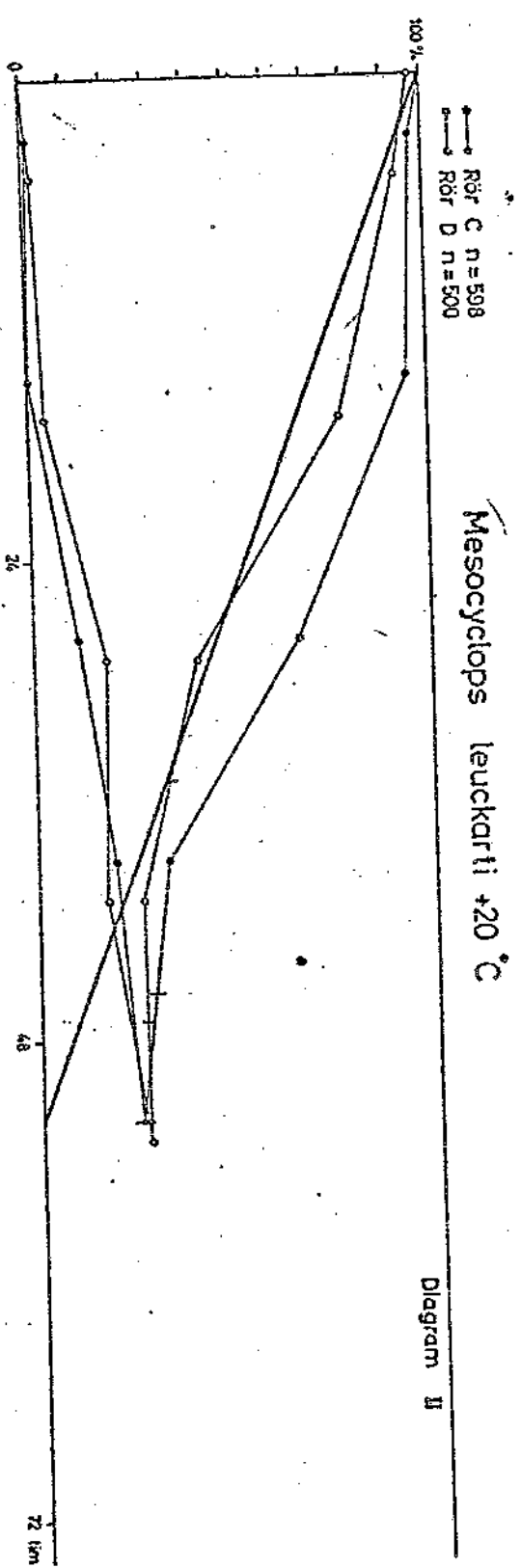
Ordinaten visar procent okläckta ägg.

Abssissan är tidsaxel.

Varje ring markerar ett observationstillfälle.



= 4.2. 2010

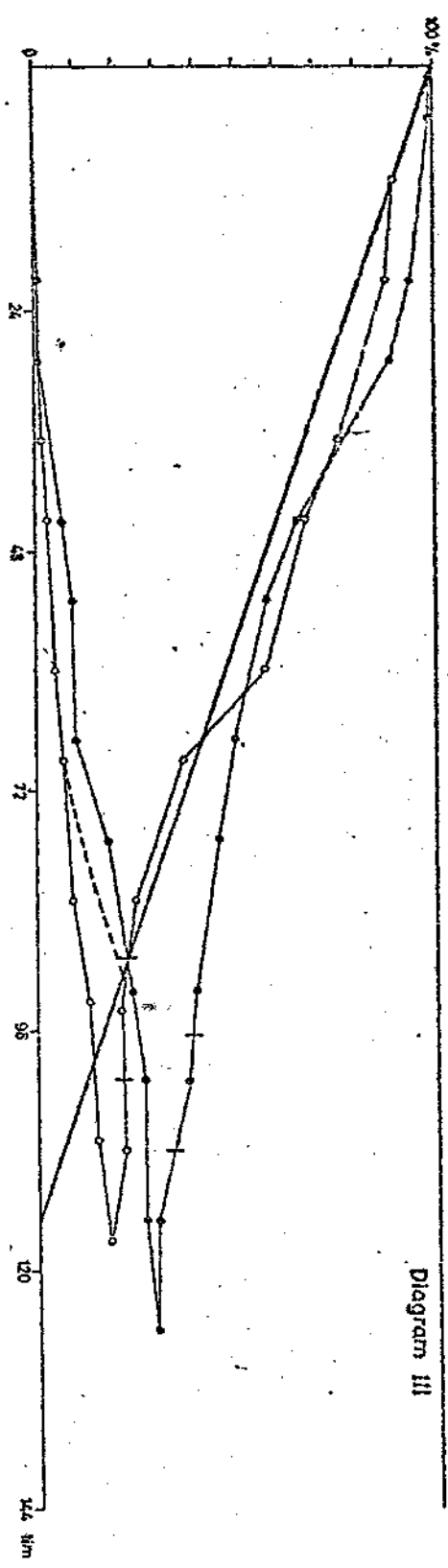


= 5.2. 2010

Rör E n=637
Rör F n=558

Mesocyclops leuckarti + 14 °C

Diagram III

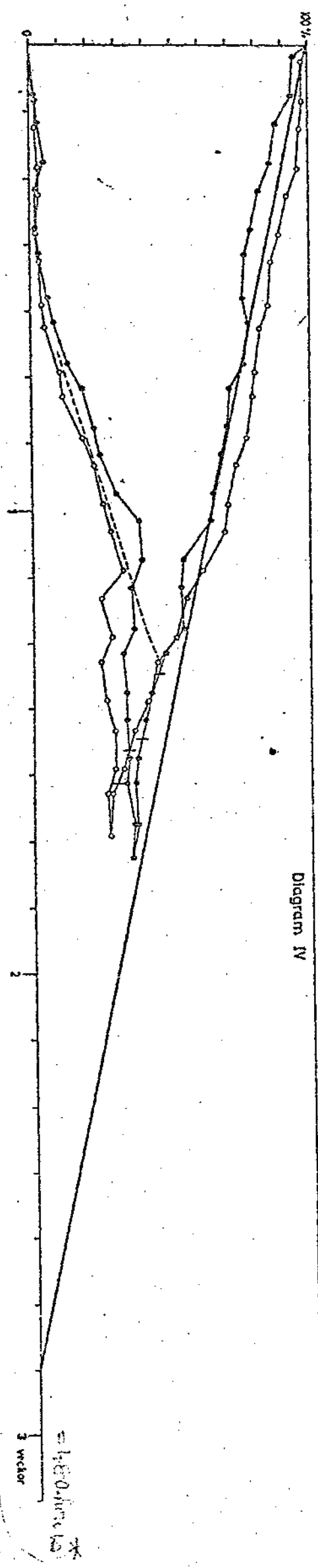


= 115 km

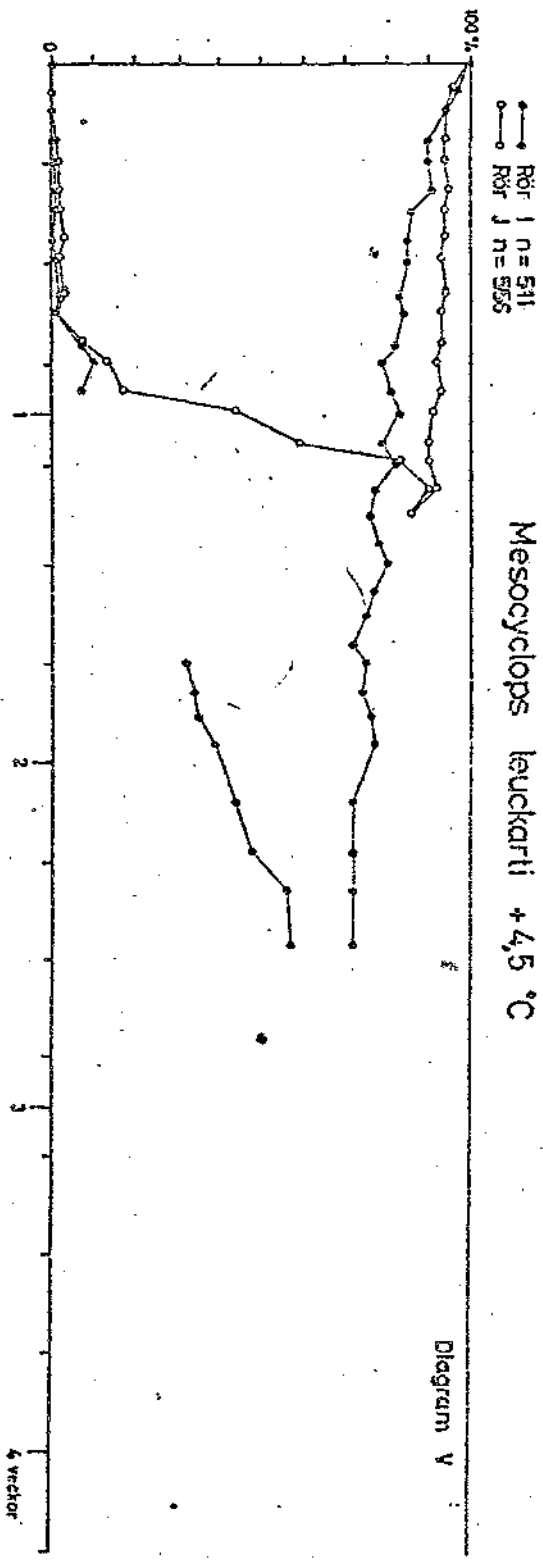
Rör G n=574
Rör H n=529

Mesocyclops leuckarti + 8 °C

Diagram IV



sub-
graph



Cyclops scutifer + 20 °C

Rör L n = 519
 Rör M n = 501
 Rör N n = 29

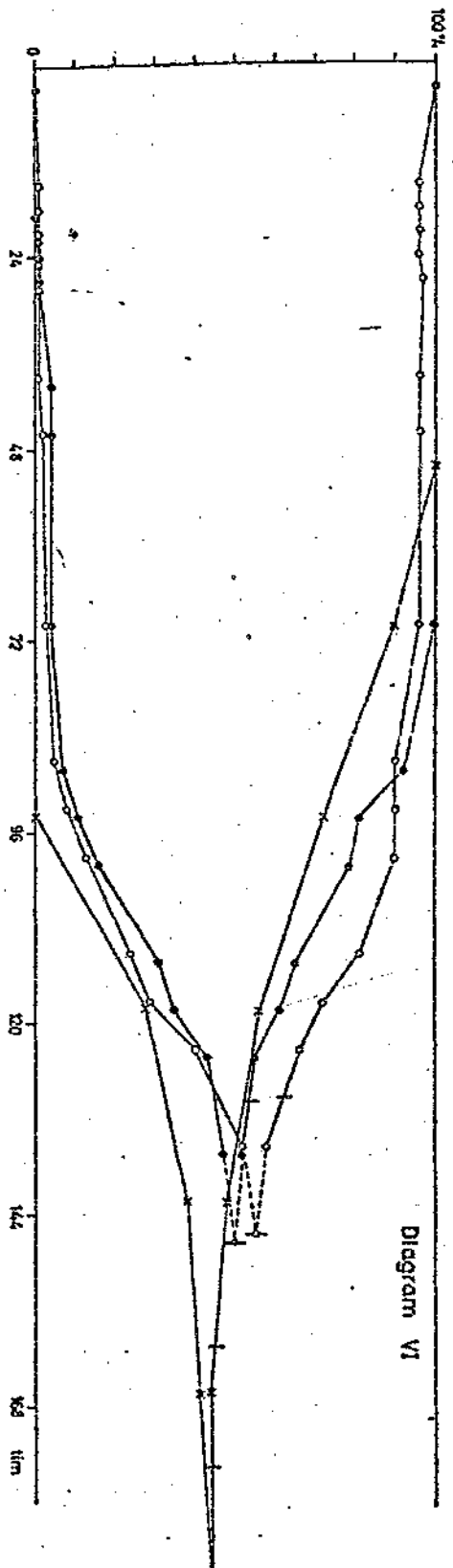


Diagram VI

Cyclops scutifer + 14 °C

Rör O n = 22
 Rör P n = 15
 Rör Q n = 46

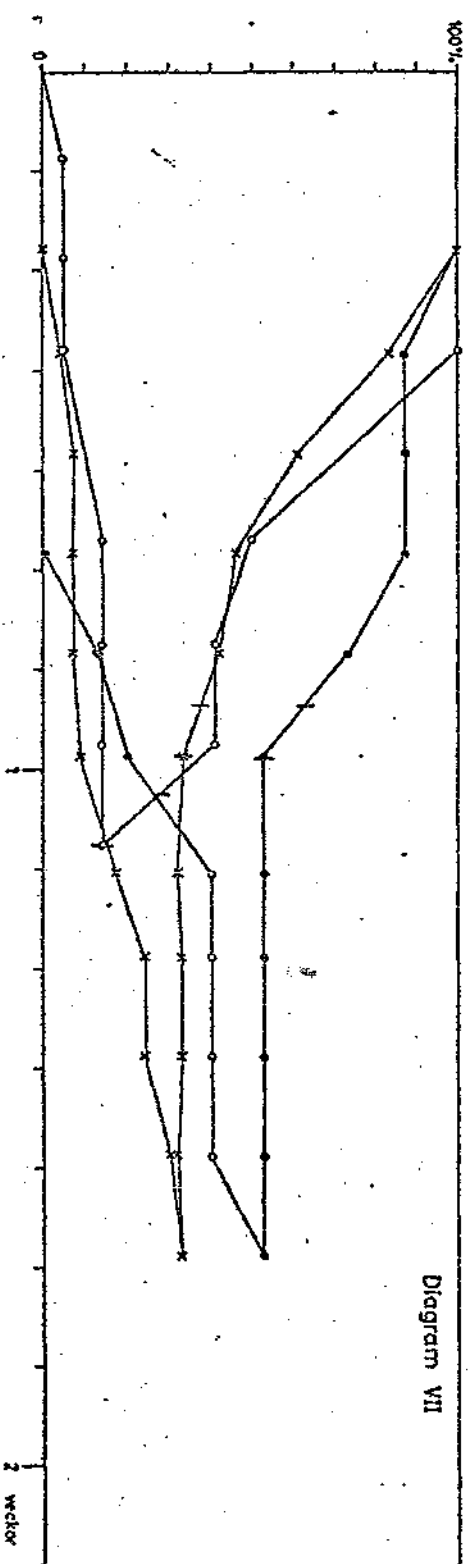


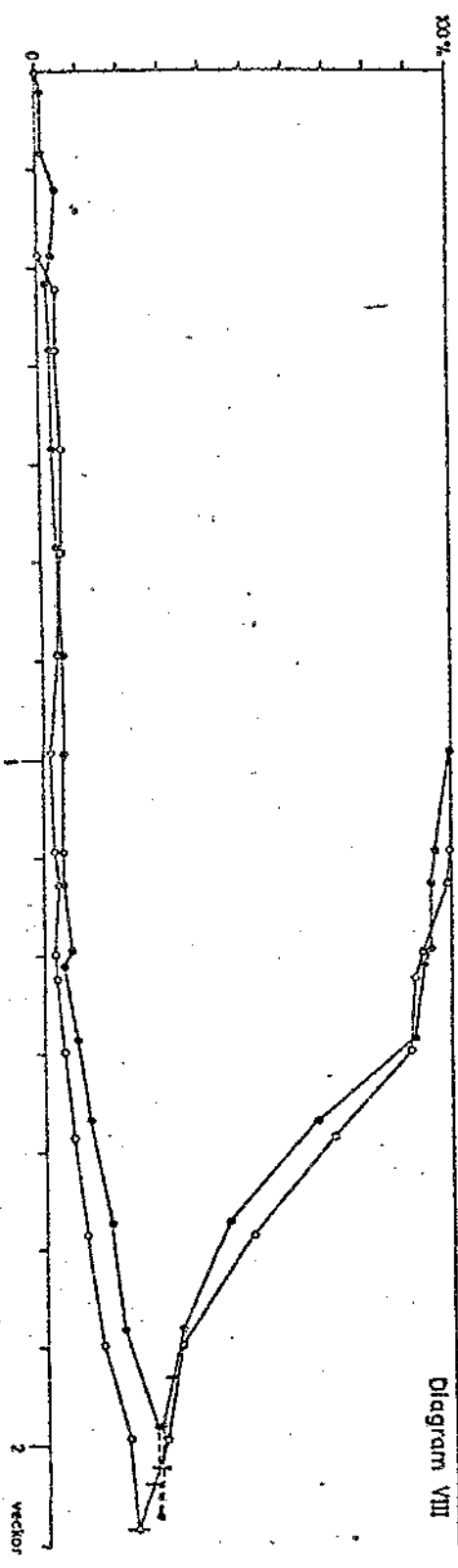
Diagram VII

2 weeks

○ Rör R n = 498
 ● Rör S n = 508

Cyclops scutifer +8°C

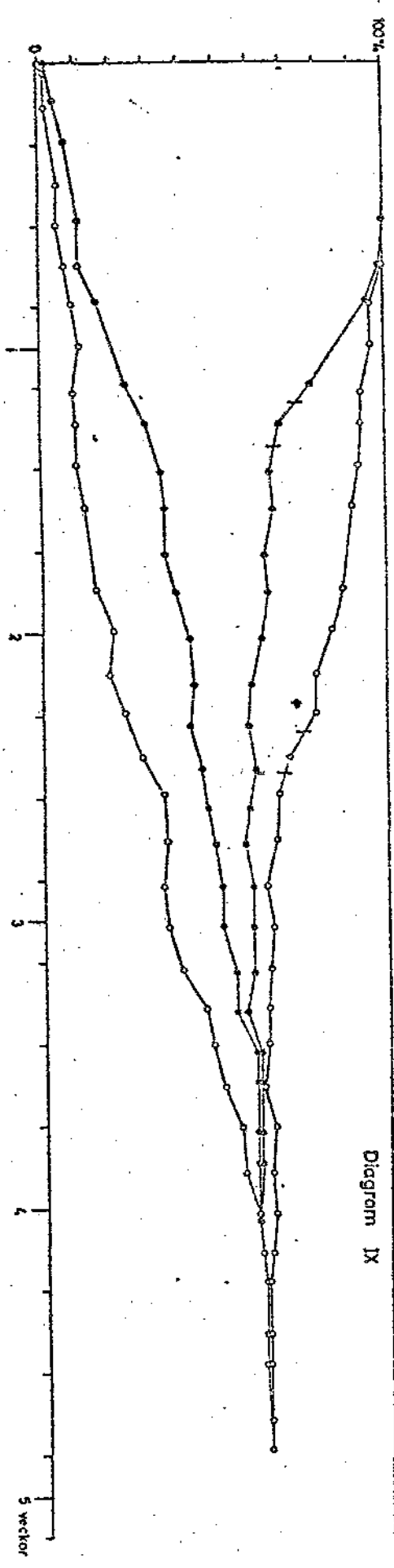
Diagram VIII



○ Rör T n = 510
 ● Rör U n = 522

Cyclops scutifer +5°C

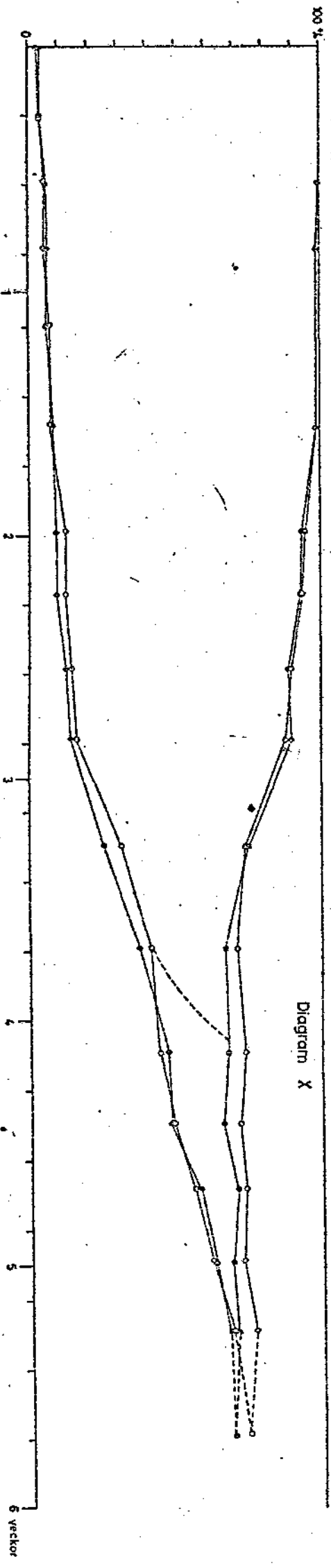
Diagram IX

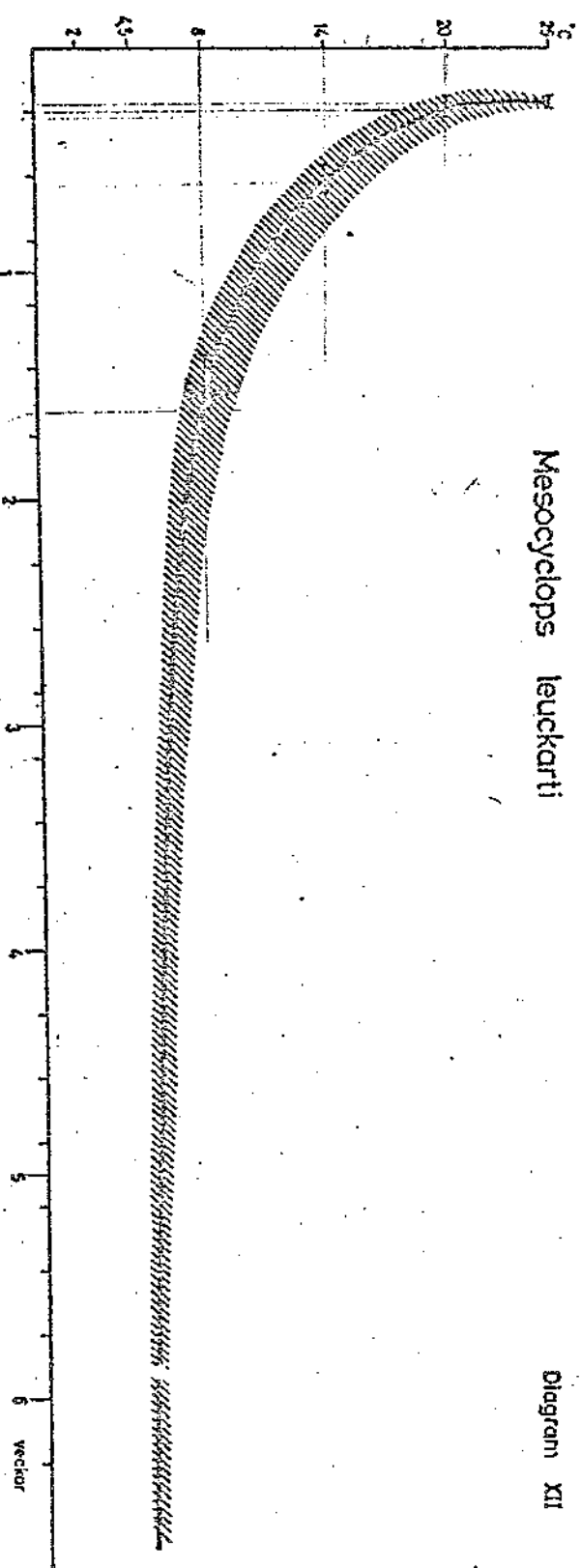
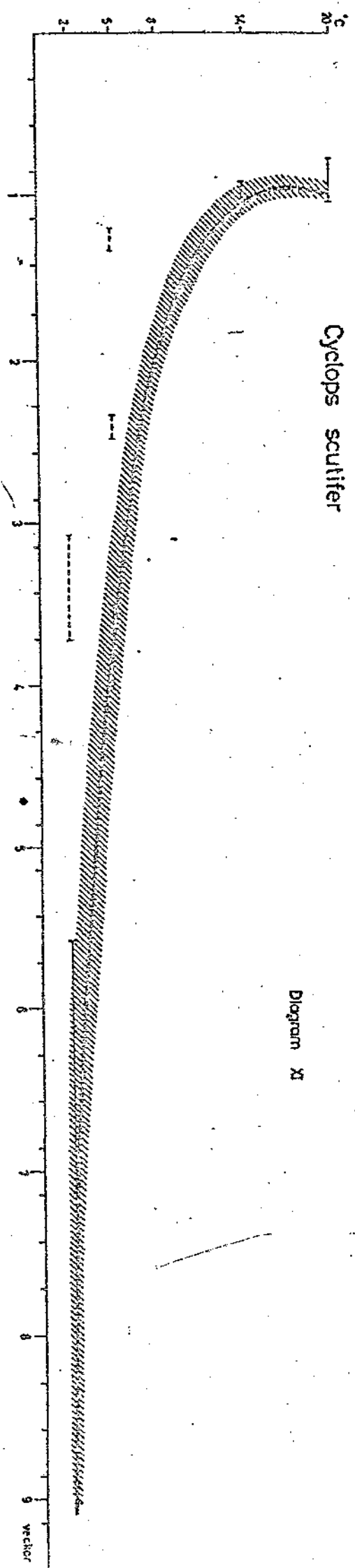


○ Rör Y n = 609
 ● Rör X n = 574

Cyclops scutifer + 2°C

Diagram X





Mesocyclops leuckarti

F ö r s ö k A + 25°C

Mesocyclops leuckartii, Erken 1/7-65

förs.start. 1/7 kl. 22.00

dag	1/7	2/7	2/7	2/7	2/7	2/7	2/7	2/7	3/7	3/7	3/7	3/7
tid	23.30	9.35	12.40	15.50	18.30	21.35	00.15	9.35	12.50	15.50	19.20	
okläckta ägg	493	447	455	395	366	326	319	124	97	39	2	
kläckta ägg	6	34	38	75	114	151	167	255	321	344	348	
döda ägg	8	13	14	16	22	22	19	122	115	127	117	
döda nauplier	0	2	2	3	6	12	12	34	47	69	91	
nauplihudar	0	0	0	0	0	0	0	0	2	2	2	
summa ägg	507	494	507	490	502	499	506	501	523	510	467	
% okläckta av Σ	97	90	90	82	73	66	63	25	17	8	0	
% kläckta av Σ	1	7	7	15	23	30	33	51	61	67	75	
% döda av Σ	2	3	3	3	4	4	4	24	22	25	25	

Hosoryflops husckarti, Erken 15/6-65

F ö r s ö k C + 20° C

Bilaga 3

förs.start. 16/6 kl. 19.00

	dag				
	16/6	17/6	17/6	18/6	18/6
tid	22.15	10.05	22.40	10.20	22.50
okläckta ägg	576	583	314	73	0
kläckta ägg	17	31	189	353	422
döda ägg	5	3	63	97	140
döda nauplier	2	4	14	23	128
naupliehudar	0	0	0	0	9
Summa ägg	598	617	566	523	562
% okläckta av Σ	96	95	56	14	0
% kläckta av Σ	3	5	33	67	75
% döda av Σ	1	0	11	19	25

Mesocyclops leuckarti, Erken 15/6-65
 förs.start. 16/6 kl. 16.30
 F ö r s ö k D + 20°C

Bilaga 4

	dag	16/6	16/6	17/6	17/6	18/6	18/6
	tid	16.45	22.00	9.45	22.15	9.45	22.15
okläckta ägg		483	478	357	101	38	0
kläckta ägg		17	38	105	251	332	340
döda ägg		0	10	19	78	77	127
döda nauplier		2	4	19	19	69	185
naupliedödar		0	0	0	0	0	14
summa ägg		500	526	481	430	447	467
% okläckta av Σ		97	91	74	23	9	0
% kläckta av Σ		3	7	22	59	74	73
% döda av Σ		0	2	4	18	17	27

Mesocyclops leuckertii, Friaan 15/6-65
 förs.start. 15/6 kl. 23.00
 F ö r s ö k E + 14°C

Bilaga 5

dag	16/6	16/6	17/6	17/6	18/6	18/6	19/6	19/6	20/6	20/6
tid	9.45	19.30	11.30	19.45	11.15	19.30	9.50	19.45	10.00	19.40
okläckta ägg	570	542	452	394	309	174	93	47	37	0
kläckta ägg	64	75	144	197	241	357	421	449	417	446
döda ägg	3	4	12	18	26	42	51	74	81	98
döda nauplier	13	5	5	3	3	7	24	48	78	90
naupliehudar	0	0	0	0	0	0	1	3	10	23
summa ägg	637	621	608	609	576	573	565	570	535	544
% okläckta av Σ	90	87	74	65	53	30	16	8	7	0
% kläckta av Σ	10	12	24	32	42	63	75	79	78	82
% döda av Σ	0	1	2	3	5	7	9	13	15	18

Hesseyelöps löschakt, Erken 15/5-65
förs.start. 16/5 kl. 15.00

F ö r s ö k F + 14°C

dag	16/5	16/5	17/5	17/5	18/5	18/5	19/5	19/5	20/5	20/5	21/5	21/5
tid	15.30	19.45	11.45	20.05	11.30	19.55	10.15	20.10	10.35	20.25	10.00	20.40
okläckta ägg	550	544	495	474	322	258	211	147	83	56	15	0
kläckta ägg	8	6	31	58	183	226	262	289	301	320	348	359
döda ägg	0	0	3	7	36	55	55	96	120	136	132	152
döda nauplier	0	2	3	6	8	10	7	12	25	42	64	88
döda nauplier	0	0	0	0	0	0	0	0	1	7	29	53
nauplieludor	0	0	0	0	0	0	0	0	1	7	29	53
summa ägg	558	550	529	539	541	539	528	532	504	512	495	511
% okläckta av Σ	99	99	93	88	59	48	40	28	16	11	3	0
% kläckta av Σ	1	1	6	11	34	42	50	54	60	62	70	70
% döda av Σ	0	0	1	1	7	10	10	18	24	27	27	30

dag	13/6	14/6	14/6	15/6	15/6	16/6	16/6	17/6	17/6	18/6	18/6	19/6	19/6	20/6	20/6	21/6	21/6	22/6	22/6	23/6
tid	20.30	10.00	20.00	10.00	20.00	10.15	20.00	12.00	20.30	11.45	20.15	10.40	20.45	11.05	21.00	10.30	21.15	11.15	20.15	10.15
okläckta ägg	564	572	568	555	526	509	493	486	449	425	407	351	306	261	236	171	178	135	116	84
kläckta ägg	10	9	20	21	47	63	83	89	107	118	121	138	163	175	180	227	254	292	323	331
döda ägg	0	3	14	17	18	14	15	22	30	62	62	104	132	145	161	189	140	168	139	146
döda nauplier	5	4	6	4	5	5	3	2	2	1	2	0	2	2	2	11	16	24	38	49
nauplienhudar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
summa ägg	574	590	602	593	591	586	591	597	586	605	590	593	601	581	577	587	572	595	578	561
% okläckta av Σ	98	96	95	93	89	87	83	81	77	70	68	59	51	45	41	29	31	23	20	15
% kläckta av Σ	2	2	3	4	8	11	14	15	18	20	21	23	27	30	31	39	45	49	56	59
% döda av Σ	0	2	2	3	3	2	3	4	5	10	11	16	22	25	28	32	24	28	24	26

dag	23/6	24/6	24/6	25/6
tid	20.40	11.00	20.00	10.45
okläckta ägg	38	16	13	1
kläckta ägg	355	363	391	371
döda ägg	158	157	141	135
döda nauplier	58	65	72	95
nauplienhudar	0	0	0	0
summa ägg	551	536	535	507
% okläckta av Σ	7	3	2	0
% kläckta av Σ	54	68	72	73
% döda av Σ	29	29	26	27

Hörsycklape Tenckartti, Erkon 12/6 1965

F ö r s ö k H + 8°C

Bilaga 8

förs.start. 13/6 kl. 17.00

dag	13/6	14/6	14/6	15/6	15/6	16/6	16/6	17/6	17/6	18/6	18/6	19/6	19/6	20/6	20/6	21/6	21/6	22/6	22/6	23/6
tid	21.00	10.30	20.30	10.30	20.30	10.40	20.15	12.15	20.45	12.05	20.35	11.00	21.05	11.25	21.20	10.50	21.35	11.40	20.45	10.40
okläckta ägg	503	515	474	430	438	415	405	301	371	351	291	257	233	189	147	82	94	94	80	46
kläckta ägg	26	32	70	76	101	114	126	132	118	130	159	157	172	190	201	243	244	248	280	303
döda ägg	0	12	17	24	13	13	19	31	42	71	100	115	131	159	215	209	181	190	172	176
döda nauplier	2	4	4	3	3	3	0	2	7	8	11	8	11	11	11	20	30	46	57	66
naupliedödar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
suena ägg	529	559	561	530	552	542	550	544	531	552	550	529	536	538	563	534	519	532	532	524
% okläckta av Σ	95	92	85	81	80	77	74	70	70	63	53	48	44	35	26	15	18	18	15	9
% kläckta av Σ	5	6	12	14	18	21	23	24	22	24	29	30	32	35	36	46	47	46	53	58
% döda av Σ	0	2	3	5	2	2	3	6	8	13	18	22	24	30	38	39	35	36	32	33

dag	23/6	24/6	24/6	25/6	25/6
tid	21.00	11.20	20.25	11.05	22.40
okläckta ägg	37	14	14	8	2
kläckta ägg	326	332	325	341	352
döda ägg	181	180	169	193	189
döda nauplier	96	99	101	114	131
naupliedödar	0	0	0	0	0
suena ägg	544	526	508	542	543
% okläckta av Σ	7	3	3	1	0
% kläckta av Σ	60	63	64	63	65
% döda av Σ	33	34	33	36	35

Mesocyclops leuckarti, Erken 12/6 1965

förs. start, 12/6 kl. 22.00

	13/6		14/6		15/6		16/6		17/6		18/6		19/6		20/6		21/6		22/6		23/6	
	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd
okläckta ägg	498	502	478	491	477	455	455	454	424	422	391	358	387	278	134	46	28	43	25	53		
kläckta ägg	13	33	51	55	45	73	78	80	92	80	95	111	97	89	101	94	115	125	119	105		
döda ägg	0	0	0	7	5	5	2	7	10	5	34	55	39	140	241	369	368	363	386	360		
döda nauplier	2	7	8	12	18	20	24	31	26	28	22	21	12	23	19	11	5	6	5	7		
nauplietuder	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
summa ägg	511	535	529	554	527	533	535	541	526	507	520	524	523	530	476	509	511	531	530	526		
% okläckta av Σ	97	94	90	89	90	85	85	84	81	83	75	69	74	0	0	0	0	0	0	0		
% kläckta av Σ	3	6	10	10	9	14	15	15	17	16	18	21	19	17	21	18	23	24	22	20		
% döda av Σ	0	0	0	1	1	1	0	1	2	1	7	10	7	0	0	0	0	0	0	0		

	23/6		24/6		25/6		26/6		27/6		28/6		29/6		30/6	
	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd	dag	tfd
okläckta ägg	39	94	152	233	217	225	202	152	130	86	87					
kläckta ägg	124	136	150	132	138	133	121	149	149	149	160					
döda ägg	375	319	231	168	180	194	204	239	260	298	327					
döda nauplier	9	9	9	13	8	11	13	14	19	22	34					
nauplietuder	0	0	0	0	0	0	0	0	0	0	0					
summa ägg	538	549	533	533	535	553	527	540	539	533	574					
% okläckta av Σ	0	0	0	43	40	41	38	28	24	16	15					
% kläckta av Σ	23	25	28	25	26	24	23	28	28	28	28					
% döda av Σ	0	0	0	32	34	35	39	44	48	56	57					

F ö r s ö k J + 4,5°C

Mesocyclops leuckarti, Erken 12/6 1955
förs.start. 12/6 kl. 24.00¹

	13/6		14/6		15/6		16/6		17/6		18/6		19/6		20/6		21/6	
	dag	tid	dag	tid	dag	tid	dag	tid	dag	tid	dag	tid	dag	tid	dag	tid	dag	tid
okläckta ägg	531	530	526	530	543	536	548	538	532	554	503	466	457	276	187	40	14	0
kläckta ägg	25	36	36	38	28	33	36	42	37	39	43	47	39	56	57	59	48	87
döda ägg	0	2	7	11	14	14	16	12	19	7	44	75	101	266	354	500	520	554
döda nauplier	6	16	16	16	18	18	14	20	15	18	21	17	15	16	11	14	5	5
naupliedöda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
summa ägg	556	568	569	587	585	583	600	592	588	600	590	588	597	598	598	593	582	641
% okläckta av Σ	96	94	93	92	93	92	91	91	91	92	86	79	76	47	31	7	2	0
% kläckta av Σ	4	6	6	6	5	6	6	7	6	7	7	8	7	9	10	10	8	14
% döda av Σ	0	0	1	2	2	2	3	2	3	1	7	13	17	44	59	83	90	86

Masocyclops leuckartii, Erken 2/9 1965

Försök K + 2°C

Bilaga 11

förs. start. 3/9 kl. 22.00

dag	4/9	6/9	8/9	12/9	15/9	19/9	21/9	23/9	25/9	28/9	30/9	2/10	3/10	4/10	5/10	6/10	7/10	9/10	11/10
tid	10.45	14.20	10.05	15.00	16.30	14.00	16.30	16.15	14.00	12.30	16.50	15.20	13.00	16.20	16.30	16.30	16.45	13.00	13.30
okläckta ägg	409	394	372	339	303	192	159	136	115	114	1357	88	61	49	49	30	45	67	19
kläckta ägg	5	15	23	38	49	52	58	54	41	48			33	37		40	31	31	31
döda ägg	4	5	13	31	61	164	193	212	228	228			284	294		301	281	263	321
döda nauplier	0	5	13	23	28	33	32	34	33	33			27	30		27	25	26	23
naupliedödar	0	0	0	0	0	0	0	0	0	0			0	0		0	0	0	0
suena ägg	418	419	406	408	413	408	410	402	384	390			378	380		371	357	367	371
% okläckta av Σ	98	95	91	83	73	47	39	34	30	29			16	13		8	13	18	5
% kläckta av Σ	1	4	6	9	12	13	14	13	11	12			9	10		11	9	8	8
% döda av Σ	1	1	3	8	15	40	47	53	59	59			75	77		81	78	74	87

dag	19/8	20/8	20/8	20/8	20/8	20/8	20/8	21/8	21/8	21/8	22/8	23/8	23/8	23/8	24/8	24/8	24/8	25/8	25/8	25/8	27/8
tid	21.10	9.30	12.05	15.30	18.25	21.10	9.45	15.40	16.10	9.10	15.30	21.05	9.20	15.35	21.10	9.40	16.00	21.15	11.00		
okläckta ägg	518	507	503	534	513	519	524	520	523	487	464	436	332	258	161	36	19	0	0		
kläckta ägg	0	22	22	21	21	17	21	21	21	59	59	55	113	172	209	263					
döda ägg	1	3	4	4	6	5	5	9	14	30	48	72	137	176	253	325					
döda nauplier	0	20	22	22	22	23	23	23	24	30	35	31	68	103	119	158		0	0	11	
naupliedödar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
summa ägg	519	532	529	559	540	541	550	530	558	576	571	563	592	606	623	624					
% okläckta av Σ	100	95	95	95	95	96	95	94	93	85	82	77	57	43	26	6					
% kläckta av Σ	0	4	4	4	4	3	4	4	4	10	10	10	19	28	34	42					
% döda av Σ	0	1	1	1	1	1	1	2	3	5	8	13	24	29	40	52					

förs.start. 19/8 kl. 17.30

dag	19/8	20/8	20/8	20/8	20/8	21/8	21/8	21/8	22/8	23/8	23/8	23/8	24/8	24/8	24/8	25/8	25/8	27/8
tid	21.50	10.00	12.35	16.10	16.10	18.55	21.40	10.10	16.05	16.30	9.45	15.00	21.35	10.00	16.15	21.55	10.20	21.30
okläckta ägg	595	619	608	613	630	628	599	605	621	556	456	421	240	174	85	31	21	0
kläckta ägg	3	4	3	3	3	3	2	3	1	52	125	138	244	261	312	314		
döda ägg	3	3	3	6	7	7	25	27	24	46	75	104	213	236	299	310		
döda nauplier	0	0	0	0	0	0	0	0	0	38	89	97	149	158	175	194		
nauplietudar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
summa ägg	601	625	614	622	640	638	626	635	646	654	656	653	697	671	696	655		
% okläckta av Σ	100	99	100	99	99	99	96	96	96	85	70	63	34	26	12	5		
% kläckta av Σ	0	1	0	0	0	0	0	0	0	8	19	21	35	39	45	48		
% döda av Σ	0	0	0	1	1	1	4	4	4	7	11	16	31	35	43	47		

F ö r s ö k N + 20 ° C

Cyclops scutiger, Länjalaure 1985

förs.start. 15/10-85 kl. 17.00

dag tid	15/10 17.00	16/10 16.00	17/10 19.00	18/10 15.00	19/10 15.00	20/10 15.00	21/10 15.00	22/10 15.00	23/10 15.00
okläckta ägg	29	29	29	26	21	8	3	1	0
kläckta ägg	0	0	0	3	8	13	15	16	16
döda ägg	0	0	0	0	0	0	11	12	13
döda nauplier	0	0	0	2	8	13	15	16	16
nauplieludor	0	0	0	0	0	0	0	0	0
summa ägg	29	29	29	29	29	29	29	29	29
% okläckta av Σ	100	100	100	90	72	28	10	3	0
% kläckta av Σ	0	0	0	10	28	44	52	56	55
% döda av Σ	0	0	0	0	0	28	38	41	45

Cyclops scutiger, latnjsaure 1965
 förs.start. 6/10 1 F ö r s ö k 0 + 14°C

	dag	6/10	7/10	8/10	9/10	11/10	12/10	13/10	14/10
	tid	20.00	17.00	17.00	15.00	13.00	14.00	14.00	14.00
okläckta ägg		8	21	21	21	8	5	6	0
kläckta ägg		0	0	0	0	11	13	13	19
döda ägg		0	1	1	1	3	3	3	3
döda nauplier		0	0	0	0	2	2	3	8
naupliohudar		0	0	0	0	0	0	0	6
summa ägg		8	22	22	22	22	22	22	22
% okläckta av	Σ	100	95	95	95	36	27	27	0
% kläckta av	Σ	0	0	0	0	50	59	59	86
% döda av	Σ	0	5	5	5	14	14	14	14

Cyclops scutiger, Lathajauru 1965
fers.start. 9/10 kl. 18.00

F ö r s ö k P + 14°

Bilaga 16

dag	9/10	11/10	12/10	13/10	14/10	15/10	16/10	17/10	18/10	19/10	20/10	21/10
tid	18.00	13.00	14.00	14.00	14.00	14.00	15.00	19.00	15.00	15.00	15.00	15.00
okläckta ägg	15	15	13	13	13	9	5	2	2	2	2	0
kläckta ägg	0	0	2	2	2	4	7	7	7	7	7	7
döda ägg	0	0	0	0	0	2	3	6	6	6	6	8
döda nauplier	0	0	0	0	2	2	2	2	2	7	7	7
nauplihudar	0	0	0	0	0	2	2	0	1	6	6	5
summa ägg	15	15	15	15	15	15	15	15	15	15	15	15
% okläckta av ΣΣ	100	100	87	87	87	60	33	13	13	13	13	0
% kläckta av ΣΣ	0	0	13	13	13	27	47	47	47	47	47	47
% döda av ΣΣ	0	0	0	0	0	13	20	40	40	40	40	53

Försök Q + 14°C

Cyclops scutiger, Latinjämnare 1965

förs.start. 9/10 kl. 16.00

dag	9/10	11/10	12/10	13/10	14/10	15/10	16/10	17/10	18/10	19/10	20/10	21/10
tid	18.00	13.00	14.00	14.00	14.00	14.00	15.00	19.00	15.00	15.00	15.00	15.00
ökläckt ägg	46	46	36	25	18	16	11	7	4	4	1	0
kläckt ägg	0	0	8	18	25	27	31	31	31	31	31	31
döda ägg	0	0	2	3	3	3	4	8	11	11	14	15
döda nauplier	0	0	0	2	4	11	21	27	30	30	31	31
nauplieludar	0	0	0	0	2	6	8	9	11	15	14	13
surra ägg	46	46	46	46	46	46	46	46	46	46	46	46
% ökläckt av Σ	100	100	79	54	39	35	24	15	9	9	2	0
% kläckt av Σ	0	0	17	39	54	58	67	68	67	67	68	67
% döda av Σ	0	0	4	7	7	7	9	17	24	24	30	33

Cyclops scutiger, Lethæa-juene 1955

Försök R + 8°C

Bilaga 18

förs.start. 19/8 kl. 13.30

	dag	19/8	20/8	21/8	22/8	23/8	24/8	25/8	26/8	27/8	27/8	28/8	28/8	29/8	30/8	31/8	1/9	2/9	3/9	7/9	
tid	19.10	10.45	19.40	11.25	19.10	10.10	10.35	11.00	12.30	12.20	12.20	20.20	12.40	19.45	13.00	9.50	10.15	12.55	12.05	10.05	13.00
okläckta ägg	495	539	531	530	519	524	519	542	548	564	568	565	532	518	502	389	250	116	54	0	0-
kläckta ägg	0	0	0	0	0	0	0	0	0	0	0	4	43	50	57	176	297	405	434	409	0-
döda ägg	0	0	0	0	23	23	29	29	24	12	18	21	20	20	32	45	64	83	121	134	0-
döda nauplier	0	0	0	0	0	0	0	0	0	0	0	0	5	18	32	60	101	141	150	197	0-
nauplihudar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	88
summa ägg	498	542	534	534	542	547	548	571	572	576	586	590	595	588	591	610	611	604	609	623	0
% okläckta av Σ	100	100	100	100	96	96	95	95	96	98	97	95	90	88	85	64	41	19	9	0	0-
% kläckta av Σ	0	0	0	0	0	0	0	0	0	0	0	1	7	9	10	29	49	67	71	78	0-
% döda av Σ	0	0	0	0	4	4	5	5	4	2	3	4	3	3	5	7	10	14	20	22	0-

Cyclops scutiger, Lathajavare 1965.

F ö r s ö k S + 8°C

Bilaga 19

förs.start. 19/8 kl. 14.30

dag	19/8	20/8	20/8	21/8	21/8	22/8	23/8	24/8	25/8	26/8	27/8	27/8	28/8	28/8	29/8	30/8	31/8	1/9	2/9	3/9
tid	20.00	11.15	20.00	11.50	19.30	10.30	10.55	11.25	12.50	12.40	12.45	20.45	13.10	20.10	13.30	10.25	10.50	13.30	12.45	11.00

okläckta ägg	501	515	480	497	504	510	501	504	518	520	500	491	503	473	445	323	171	85	7	0
kläckta ägg	0	0	0	0	0	0	0	0	0	0	21	27	28	39	50	193	333	418	441	
döda ägg	5	4	18	18	12	18	18	23	25	28	30	30	37	29	41	67	96	118	167	
naupliar	0	0	0	0	0	0	0	0	0	0	5	15	22	34	45	104	222	320	343	
svana ägg	508	521	501	515	516	528	519	528	543	548	551	548	558	541	535	523	600	621	615	
% okläckta av Σ	99	99	96	97	98	97	97	96	95	95	91	90	88	88	83	56	29	14	1	
% kläckta av Σ	0	0	0	0	0	0	0	0	0	0	4	5	5	7	9	33	55	67	72	
% döda av Σ	1	1	4	3	2	3	3	4	5	5	5	5	7	5	8	11	16	19	27	

dag	7/9	8/9	9/9	10/9
tid	13.00	11.00	10.00	13.00

naupliar	0	0	0	2
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Cyclops scutiger, latnajauna 1965

F o r s ö k T + 5°C

Bilaga 20

förs.start. 24/8 kl. 15.00

dag	24/8	25/8	27/8	28/8	29/8	30/8	31/8	1/9	2/9	3/9	4/9	6/9	7/9	8/9	9/9	10/9	11/9	12/9	13/9	14/9
tid	20.30	17.05	13.55	14.10	14.00	12.40	12.55	17.00	10.40	11.00	16.15	11.30	10.30	13.25	10.45	13.15	11.15	14.25	17.15	16.55
okläckta ägg	508	511	508	495	501	473	466	454	441	448	426	397	363	340	306	249	200	182	177	179
kläckta ägg	0	0	3	0	2	20	20	41	39	43	52	73	92	118	114	172	191	167	212	195
döda ägg	10	10	26	25	35	47	62	49	54	57	63	85	112	109	125	165	197	194	198	203
döda nauplier	0	0	0	0	1	15	22	38	41	39	48	52	62	75	77	104	98	123	122	135
nauplihudar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
susna ägg	518	521	537	520	538	540	570	544	534	548	541	555	567	567	545	586	588	563	587	577
okläckta av Σ	98	98	94	95	93	87	85	84	83	82	78	72	64	60	56	43	34	32	30	31
kläckta av Σ	0	0	1	0	0	4	4	7	7	8	10	13	16	21	21	29	32	33	36	34
döda av Σ	2	2	5	5	7	9	11	9	10	10	12	15	20	19	23	28	34	35	34	35

dag	15/9	16/9	17/9	18/9	19/9	20/9	21/9	22/9	23/9	24/9	25/9	26/9	27/9
tid	18.20	17.15	14.10	15.15	15.10	16.05	17.30	16.55	9.45	16.45	10.30	19.45	13.00
okläckta ägg	143	102	88	67	55	40	26	15	5	4	4	2	0
kläckta ägg	191	199	200	209	182	179	175	180	183	183	183	183	103
döda ägg	213	251	262	295	300	297	320	319	326	327	327	329	331
döda nauplier	145	144	149	138	139	156	141	168	171	171	171	171	171
nauplihudar	0	0	0	0	0	0	0	0	0	0	0	0	0
susna ägg	547	552	550	571	537	516	521	514	514	514	514	514	514
okläckta av Σ	26	18	16	12	10	8	5	3	1	1	1	0	0
kläckta av Σ	35	36	36	37	34	35	34	35	36	36	36	36	36
döda av Σ	39	46	48	51	56	57	61	62	63	63	63	64	64

Cyclops scutiger, Lathjafjære 1965

förs.start. 24/8 kl. 15.00

Försök U + 5°C

Bilaga 21

dag	24/8	25/8	27/8	28/8	29/8	30/8	31/8	2/9	3/9	4/9	6/9	7/9	8/9	9/9	10/9	11/9	12/9	13/9	14/9
tid	20.00	16.40	13.30	13.45	14.30	12.10	12.30	10.10	12.50	9.45	11.05	10.00	13.00	10.15	13.00	11.00	14.00	17.00	16.30
okläckta ägg	608	602	601	600	552	528	502	487	472	443	312	225	191	181	175	157	125	104	102
kläckta ägg	4	1	1	1	0	4	2	2	3	25	128	178	205	186	212	200	215	245	251
döda ägg	10	12	21	19	11	22	38	58	60	86	139	176	200	199	210	214	244	257	264
döda nauplior	0	0	0	0	0	0	0	0	0	6	54	82	106	111	112	117	117	124	124
naupliohudar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
summa ägg	622	615	623	620	563	554	542	547	535	554	579	579	596	565	597	571	584	606	617
% okläckta av Σ					98	95	93	89	88	79	54	39	32	32	29	27	21	17	17
% kläckta av Σ					0	1	0	0	1	5	22	31	34	33	36	35	37	40	41
% döda av Σ					2	4	7	11	11	16	24	30	34	35	35	38	42	43	42

dag	15/9	16/9	17/9	18/9	19/9	20/9	21/9	22/9	23/9	24/9	25/9	26/9
tid	18.00	17.00	14.00	15.00	15.00	17.45	17.15	16.30	9.45	16.30	10.30	19.45
okläckta ägg	93	69	56	55	51	30	16	6	6	6	6	0
kläckta ägg	234	245	249	235	233	236	239	210	210	210	210	211
döda ägg	272	278	289	295	299	317	318	331	331	331	331	336
döda nauplior	121	130	139	135	130	133	141	139	139	139	139	139
naupliohudar	0	0	0	0	0	0	0	0	0	0	0	0
summa ägg	599	592	594	585	583	583	573	547	547	547	547	547
% okläckta av Σ	16	12	9	9	9	5	3	1	1	1	1	0
% kläckta av Σ	39	41	42	40	40	40	42	38	38	38	38	39
% döda av Σ	45	47	49	51	51	55	55	61	61	61	61	61

Cyclops scutiger, Laitinjauhe 1955

F ö r s ö k V + 2°C

förs.start. 23/8 kl. 17.30

Bilaga 22

dag tid	24/8 16.45	25/8 17.30	27/8 15.30	29/8 13.00	31/8 16.25	3/9 13.15	6/9 14.35	8/9 10.20	10/9 14.10	12/9 15.10	15/9 16.45	18/9 16.00	21/9 16.00	23/9 16.45	25/9 14.15	27/9 16.30	29/9 16.20
okläckta ägg	593	589	581	610	568	576	538	532	492	461	294	202	179	141	101	60	42
kläckta ägg	0	0	0	4	0	5	34	36	64	76	174	192	161	172	151	147	130
döda ägg	16	22	38	33	40	44	79	75	88	103	209	278	283	291	324	340	385
döda nauplier	0	0	0	0	0	2	13	13	23	38	80	124	134	154	154	154	145
naupliedöda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
summa ägg	609	611	619	647	608	625	651	643	644	640	677	672	623	604	576	547	557
% okläckta av Σ	97	96	94	94	93	92	83	82	76	72	43	30	29	23	18	11	8
% kläckta av Σ	0	0	0	1	0	1	5	6	10	12	26	29	26	26	26	27	23
% döda av Σ	3	4	6	5	7	7	12	12	14	16	31	41	45	49	56	62	69

dag tid	30/9 16.30	1/10 16.40	2/10 15.20	3/10 13.00
okläckta ägg	29	3	1	0

F ö r s ö k X + 2°C

Cyclops scutiger, Letnajaure 1965

förs.start. 23/8 kl. 17.30

dag	24/8	25/8	27/8	29/8	31/8	3/9	6/9	8/9	10/9	12/9	15/9	18/9	21/9	23/9	25/9	27/9	29/9
tid	17.10	18.00	15.50	13.20	17.05	13.10	15.30	10.40	14.30	15.30	17.00	16.25	16.15	17.00	14.30	16.45	16.40
okläckta ägg	552	558	556	500	546	542	515	505	462	455	295	192	123	100	69	34	16
kläckta ägg	0	0	0	4	0	8	35	35	63	60	153	207	186	189	152	164	150
döda ägg	22	21	36	36	35	48	52	54	74	81	155	231	278	260	312	328	353
döda neoplter	0	0	0	0	0	7	25	29	44	45	35	163	178	191	182	189	184
neopltehudar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
suama ägg	574	579	592	528	581	598	602	595	599	596	603	630	587	549	533	526	519
% okläckta av Σ	96	96	94	93	94	91	85	85	77	76	50	30	21	18	13	6	3
% kläckta av Σ	0	0	0	1	0	1	6	6	11	10	25	33	32	34	29	31	29
% döda av Σ	4	4	6	6	6	8	9	9	12	14	25	37	47	48	58	63	68

dag	30/9	1/10	2/10	3/10
tid	16.40	16.50	15.20	13.00

okläckta ägg	16	15	11	0
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Notice

Please note that these translations were produced to assist the scientific staff of the FBA (Freshwater Biological Association) in their research. These translations were done by scientific staff with relevant language skills and not by professional translators.